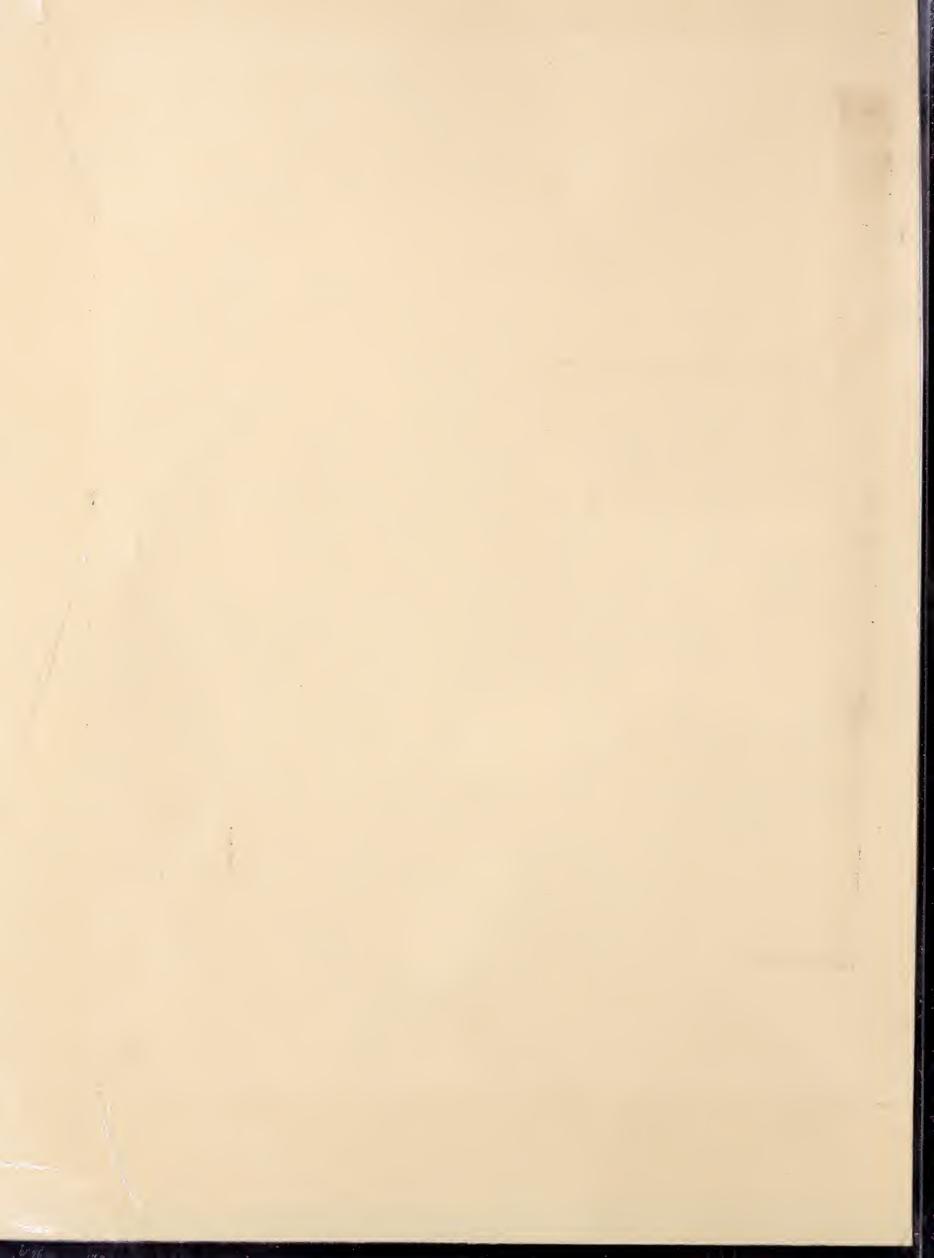
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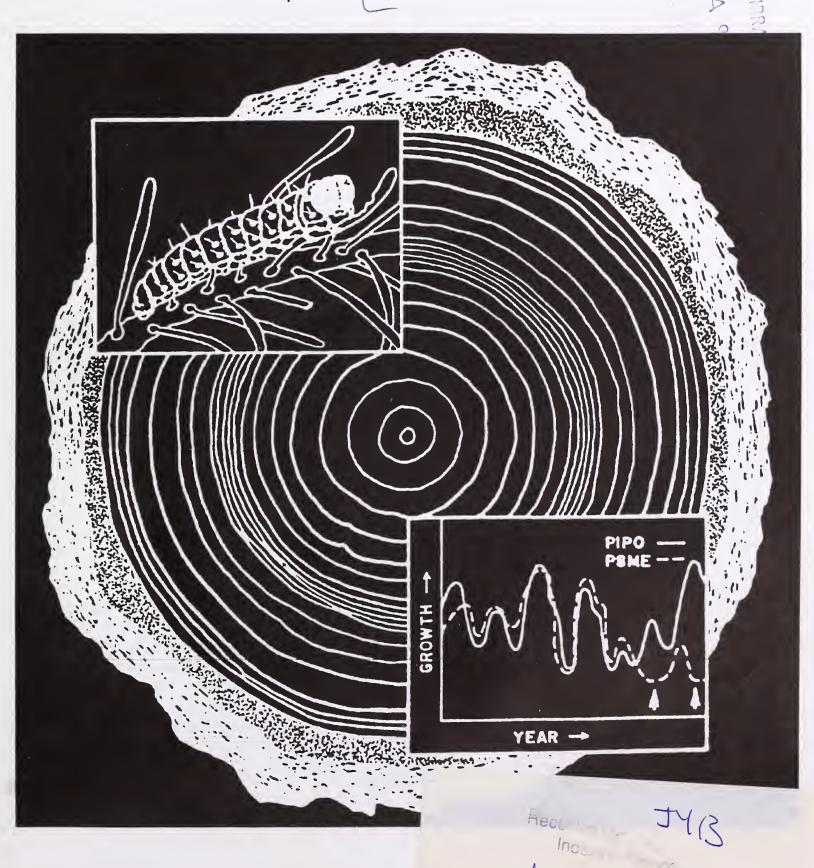
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Historical Patterns of Western Spruce Budworm and Douglas-Fir Tussock Moth Outbreaks in the Northern Blue Mountains, Oregon, Since A.D. 1700

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Abstract

Swetnam, Thomas, W.; Wickman, Boyd E.; Paul, H. Gene; Baisan, Christopher H. 1995. Historical patterns of western spruce budworm and Douglas-fir tussock moth outbreaks in the northern Blue Mountains, Oregon, since A.D. 1700. Res. Pap. PNW-RP-484. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 27 p.

Dendroecology methods were used to reconstruct a three-century history of western spruce budworm and Douglas-fir tussock moth outbreaks in the Blue Mountains of northeastern Oregon. Comparisons of 20th century Forest Service documentary records and host and nonhost tree-ring width chronologies provided an objective basis for distinguishing climatic effects from insect-caused defoliation effects. Budworm outbreaks were more confidently reconstructed than were tussock moth outbreaks. Since A.D. 1700, at least eight regional budworm outbreaks have occurred at intervals of about 21 to 53 years. Reduced radial growth caused by defoliation lasted from about 13 to 17 years. Two regional budworm outbreaks occurred during the 19th century, and at least three and possibly four regional outbreaks have occurred during the 20th century. These findings generally support the hypothesis that budworm outbreaks have increased in frequency and severity in the 20th century in northeastern Oregon.

Keywords: Western spruce budworm, Douglas-fir tussock moth, tree rings, Blue Mountains, forest health, dendroecology.

Summary

Tree-ring samples from 21 mixed-conifer stands in the Blue Mountains of northeastern Oregon were analyzed for evidence of past western spruce budworm and Douglas-fir tussock moth outbreaks. Comparison of host and nonhost tree-ring growth provided an objective basis for distinguishing climatic effects from insect defoliation effects. Different rates and duration of attack by budworm and tussock moth, and the resulting differences in tree-ring growth patterns, provided a basis for reconstructing a 300-year history of outbreaks of both insect species. We were not completely successful at separating the effects of the two species in the analyzed tree-ring series, and budworm outbreaks were more confidently reconstructed than were tussock moth outbreaks. Our reconstruction shows that since ca. A.D. 1700 at least eight regional budworm outbreaks have occurred at intervals of about 21 to 53 years. Reduced radial growth periods caused by defoliation lasted from 13 to 17 years. Two regional budworm outbreaks occurred in the 19th century (ca. 1806 to 1822 and ca. 1851 to 1867), three outbreaks occurred in the northern Blue Mountains in the 20th century (ca. 1898 to 1910, ca. 1946 to 1958, and ca. 1980 to present), and an additional outbreak occurred in the Eagle Cap Wilderness (ca. 1925 to 1939). It is unlikely that the high mortality rates (often exceeding 80 percent) observed during the most recent outbreak could have been sustained in the many previous outbreaks recorded in our sampled stands. These findings generally lend support to the hypothesis that budworm outbreaks have increased in frequency and severity in the 20th century in northeastern Oregon. Additional reconstructions are needed to test the influence of spatial and temporal scales of observation on assessments of outbreak regime changes as well as interactions with fire, climate, and land-use history.



Introduction

Forests of northeastern Oregon have been repeatedly defoliated by outbreaks of western spruce budworm (*Choristoneura occidentalis* Freeman) and Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough) (Dolph 1980; Wickman and others 1973, 1980, 1994). Recent, severe outbreaks of these insects in the Blue Mountains have focused the attention of managers and scientists at both regional and national levels on "forest health" problems (Gast and others 1991, Wickman 1992, Wickman and others 1994). Proposals currently are being debated that would use large-scale prescribed burning and silvicultural treatments as primary ecosystem management tools to re-establish more stable and sustainable forest structures and processes (Mutch and others 1993). The management decisions and plans that are ultimately pursued in the Blue Mountains may establish a highly visible precedent and guide for other regions of the United States suffering similar catastrophic insect outbreaks, pathogen epidemics, or fires.

Forest tree and insect population dynamics operate over time scales ranging from seasons to centuries and spatial scales from individual trees to landscapes. A solid knowledge base of past natural and human-caused disturbances across this range of scales is essential for determining if, in fact, current forest disturbance regimes and ecosystems have changed or become unstable and unsustainable. Historical knowledge of the "natural range of variability" of ecosystem disturbances is valuable for understanding how current forest structures were created, and for identifying processes and patterns that either sustain ecosystems over long periods of time or lead to their demise (Morgan and others 1994, Swanson and others 1994).

Western spruce budworms and Douglas-fir tussock moths are both native to the Blue Mountains region, but the severity and extensiveness of tree mortality during outbreaks in the late 20th century suggest that their dynamics have changed. The leading hypothesis is that past land use practices, especially forest harvesting of nonhost species and fire suppression, have led to dense, multistoried stands dominated by shade-tolerant host tree species, and that these stands are more susceptible and vulnerable to defoliator outbreaks than were presettlement forests (Mutch and others 1993, Wickman 1992). Similar hypotheses and evidence have been offered for observed budworm outbreak changes in the northern Rocky Mountains (Anderson and others 1987, Carlson and others 1985, Fellin and others 1983, McCune 1983, Schmidt 1985) and in the southern Rockies (Swetnam and Lynch 1989, 1993). Conversely, in a review of possible interactions of landscape patterns and forest pest outbreaks in the Pacific Northwest, Perry (1988) states that there is little evidence to support the hypothesis that landscape changes caused by natural or human factors resulted in increased pest problems. Perry's review concentrated mainly on forests west of the Cascade Range.

Specific tests of outbreak-change hypotheses for the Blue Mountains of Oregon had not been attempted prior to our work. In the 20th century, both western spruce budworm and Douglas-fir tussock moth populations have erupted in outbreaks separated by several years to several decades (Dolph 1980, Mason and Wickman 1989, Wickman and others 1973), but the frequency, extent, and severity of outbreaks in earlier centuries are unknown. At least a two-century time perspective is needed to evaluate the role of budworm and tussock moth in the presettlement era (before about 1870) relative to the settlement and postsettlement eras when extensive logging, live-stock grazing, and fire suppression began. Additionally, knowledge of historical pat-

terns of land use and climatic variations is needed to identify potential interactions of these external, regional-scale factors with the internal, local-scale factors controlling insect and tree population dynamics (Swetnam and Lynch 1993).

The objectives of this study were to reconstruct and analyze a multicentury history of budworm and tussock moth outbreaks in old-growth mixed-conifer stands of the northern Blue Mountains and Eagle Cap Wilderness in northeastern Oregon. We were particularly interested in assessing possible changes in outbreak dynamics in the 20th century relative to previous centuries. Our starting point for this study was observations of radial growth responses to defoliation by these two insects in previous treering studies conducted within the region (Brubaker 1978; Brubaker and Greene 1979; Wickman 1980, 1986). From this work it was evident that characteristic tree-ring patterns (hereafter called signatures) caused by budworms and tussock moths might be detected and isolated in radial increment time series. Following this lead, we applied dendrochronological methods developed and demonstrated in the southern Rocky Mountains (Swetnam and others 1985; Swetnam and Lynch 1989, 1993) to tree-ring collections from the Blue Mountains. In this paper, we describe the results of our investigations in the northern Blue Mountains; we focused primarily on the historical patterns of change in regional-scale outbreaks among all sampled stands.

Twenty-one mixed-conifer stands were sampled in the northern Blue Mountains (fig. 1). All stands were in the Umatilla and Wallowa-Whitman National Forests. The mixed-conifer stands generally were dominated by grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), with smaller components of other conifer species, such as ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) (table 1). Old-growth stands with little or no history of past logging directly within the sampled area were selected so that maximum length tree-ring records would be obtained.

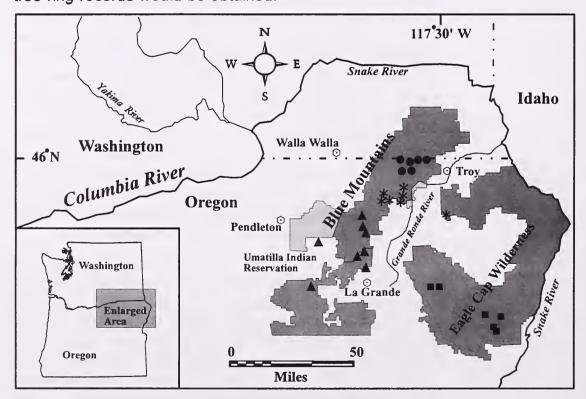


Figure 1—Locations in northeastern Oregon of sampled mixed-conifer and ponderosa pine stands. Symbols denote locations of different groups of sampled stands: Blue Mountains-Wenaha = dots; Blue Mountains-Big Sink = asterisks; Blue Mountains-Oregon Trail = triangles; Eagle Cap = squares.

Table 1—Basal area and percentages of tree species within sampled mixed-conifer stands

	Basal area by species ^a							
Site name	ABGR	PSME	PIPO	LAOC	PIEN	PICO	TABR	Total
			- Square	meters	per hec	tare ^b –		
Blue Mountains, Wenaha:								
Wenaha 1	39.7 (68)	9.0 (15)	10.1 (17)					58.8
Wenaha 2	26.6 (56)	12.9 (27)	8.3 (17)					47.8
Soap Springs	21.6 (60)	7.1 (20)	6.4 (18)	0.9 (3)				36.0
Grizzly Bear Meadow	46.8 (65)	4.6 (6)	9.2 (13)	11.9 (16)				72.6
Blue Mountains, Big Sink:								
Big Sink	38.6 (76)	3.7 (7)		2.8 (5)	5.5 (11)			50.5
East Big Sink	9.2 (22)	2.3 (6)	29.8 (72)					41.3
Lookout Mountain	72.1 (98)			1.6 (2)				73.7
Summit Spring	23.0 (59)	9.9 (25)	1.6 (4)		3.9 (10)	0.7 (2)		39.0
Blue Mountains, Oregon Tr	ail:							
High Ridge	50.5 (73)	5.5 (8)		2.8 (4)	10.1 (15)			68.9
Ruckles Junction	46.2 (98)	.3 (1)			.5 (1)			46.9
Dry Creek	38.6 (71)	4.6 (8)		1.8 (3)	7.3 (14)		1.8 (3)	54.2
Green Mountain	62.5 (89)		.9 (1)	.9 (1)	5.5 (8)			69.8
Drumhill Ridge	58.8 (88)	6.0 (9)		1.8 (3)	.2		ı	66.8
Mount Emily	28.5 (60)	17.4 (37)	1.8 (4)					47.8

Table 1—Basal area and percentages of tree species within sampled mixed-conifer stands (continued)

Site name	Basal area by species ^a							
	ABGR	PSME	PIPO	LAOC	PIEN	PICO	TABR	Total
			- Square	e meters	per hec	tare ^b –		
Emigrant Springs	24.5 (38)	31.6 (48)	9.2 (14)					65.3
Bally Mountain	19.4 (72)	2.8 (11)	1.2 (5)	3.4 (13)				26.8
Eagle Cap, West:								
Minam River	36.0 (77)	.7 (2)		3.0 (7)	5.3 (11)	.7 (2)	0.7 (2)	46.6
North Fork Minam River	64.3 (81)	0.7 (1)			14.4 (18)			79.4
Eagle Cap, East:								
Imnaha River N. Fork	40.4 (56)	21.1 (29)	1.8 (3)	6.4 (9)	.9 (1)	.9 (1)		71.6
Indian Crossing	24.8 (50)	8.3 (17)	14.7 (30)	1.8 (4)				49.6
Fish Lake	28.0 (71)	3.2 (8)	8.3 (21)					39.5

^a Species codes:

ABGR = Abies grandis
PSME = Pseudotsuga menziesii
PIPO = Pinus ponderosa
LAOC = Lanx occidentalis
PIEN = Picea engelmannii
PICO = Pinus contorta
TABR = Taxus brevifolia

^b Values in parentheses are percentages.

Increment Core Collections

A total of 175 Douglas-fir, 251 grand fir, and 170 ponderosa pine trees were sampled (table 2) by taking two increment cores from each tree on opposite sides of the stem at approximately breast height (1.37 m). Tree-ring chronologies from the ponderosa pine (nonhost species) were used as climatic controls in analysis of the chronologies from the Douglas-fir and grand fir (host species) (see "Laboratory Analysis," below). When present, both Douglas-fir and grand fir were sampled in each mixed-conifer stand to develop a tree-ring width chronology for each host species. Some stands contained relatively few mature Douglas-fir, so only grand fir chronologies were developed for these stands (table 1). Whenever possible, ponderosa pine were sampled for development of nonhost chronologies in separate, but nearby stands (within one to a few kilometers of the mixed-conifer stands) dominated by this species. In a few cases, no nearby ponderosa pine-dominated stands could be located, so pines were sampled within the mixed-conifer stands sampled for the host chronologies. The stands were sampled systematically by following meandering transects along topographic contours and taking increment cores from the largest dominant and codominant trees as they were encountered along the transect. Sampled trees within stands were distributed over areas of about 5 to 10 ha.

Laboratory Analysis

Dendrochronology procedures for preparing and analyzing ring-width data for evaluation of insect defoliation effects are described and illustrated by Swetnam and others (1985) and Swetnam and Lynch (1989, 1993). The basic strategy of these procedures is to develop well-dated, standardized tree-ring width chronologies from both host (Douglas-fir and grand fir in this case) and nonhost trees (ponderosa pine) and to use the nonhost chronologies to remove the climatic signal from the host chronologies. This is accomplished by a differencing procedure, where rescaled nonhost chronologies are subtracted from the host chronologies. A "corrected" (residual) host series is produced that retains ring-growth variations resulting primarily from effects of past defoliation episodes and recovery after these episodes. Necessary conditions, assumptions, and testing of these procedures are discussed in detail in the papers cited above. In brief, the procedures were as follows:

- 1. All increment cores were mounted in wooden core holders and surfaced with very fine sandpaper (up to 400 grit).
- 2. Ring widths were measured on a sliding-stage incremental measuring machine.
- 3. Crossdating was accomplished by a combination of the skeleton plot method (Stokes and Smiley 1968) and application of the COFECHA crossdating and quality control computer program (Holmes 1986). The COFECHA program was used to check the dated and measured ring-width series for possible errors in the initial dating or measurements and to make corrections if required.
- 4. Ring-width series for each core were standardized (that is, transformed) into dimensionless indices by fitting a growth curve to the series and then dividing the ring widths by the values of the fitted curve (Fritts 1976, Swetnam and others 1985). This procedure removed long-term growth trends related primarily to tree aging or bole geometry, but retained relatively short-term growth fluctuations related to insect defoliation or climatic variations. A 50-percent frequency-response cubic smoothing spline of 100 years was fit to all core series (Cook and Holmes 1986, Cook and Peters 1981). This type of cubic spline removes most ring-width trends extending over periods greater than about 100 years. Thus, growth reductions caused by budworm outbreaks, which usually continue for less than 20 years (Dolph 1980), and

Table 2—Species and numbers of trees sampled in each stand

Stand name	ID ^a	Species ^b	No. of trees	Inner date ^c	Outer date
Blue Mountains, Wenaha:					
Wenaha 1	WH1D	PSME	15	1730	1991
	WH1P	PIPO	4	1714	1991
Wenaha 2	WH2D	PSME	7	1819	1991
	WH2G	ABGR	7	1841	1991
Soap Springs	SOSG	PSME/ABGR	20	1784	1990
	SOPP	PIPO	10	1623	1990
Grizzly Bear Meadow	GBMD	PSME	22	1672	1991
	GBMG	ABGR	21	1690	1991
Grizzly Bear Ridge	GBRP	PIPO	18	1502	1991
Cross Canyon Trailhead	CCTP	PIPO	17	1485	1991
Blue Mountains, Big Sink:					
Big Sink	BSKD	PSME	6	1797	1990
	BSKG	ABGR	28	1812	1990
East Big Sink	EBSP	PIPO	21	1665	1990
Lookout Mountain	LO2G	PSME/ABGR	15	1799	1990
	LO2P	PIPO	10	1665	1990
	LO4G	ABGR	15	1802	1990
Luger Springs	LSPP	PIPO	11	1675	1991
Summit Spring	SSPD	PSME	8	1830	1990
	SSPG	ABGR	9	1848	1990
	SSPP	PIPO	12	1760	1990
Blue Mountains, Oregon Trail:					
High Ridge	HIRD	PSME	2	1887	1990
	HIRG	ABGR	12	1814	1990
Ruckles Junction	RKJD	PSME	1	1853	1990
	RKJG	ABGR	21	1789	1990
Dry Creek	DCKD	PSME	3	1751	1990
	DCKG	ABGR	10	1860	1990
Green Mountain	GMTD	PSME	2	1728	1991
	GMTG	ABGR	19	1740	1991
Drumhill Ridge	DHRD	PSME	9	1808	1990
	DHRD	ABGR	6	1799	1990
	DHRP	PIPO	5	1672	1990
Mount Emily	MTED	PSME	14	1720	1991
	MTEG	ABGR	3	1879	1991
Emigrant Springs	ESPD	PSME	21	1738	1990
	ESPG	ABGR	11	1813	1990
	ESPP	PIPO	10	1761	1990

Erratum

Table 4 on p. 21 has a datum error, shown in bold here. We apologize for any inconvenience to the reader.

Table 4—Estimate of timing, duration, and intervals between western spruce budworm outbreaks from tree-ring chronologies

				Intervals between outbreaks ^b		
Outbreak period	Peak year ^a	Outbreak duration	Initial	Peak		
Modern, known outbreaks:		No. of y	ears			
1980 to present	1986	- 14	34	36		
1946 to 1958	1950	13	21	16		
Inferred outbreaks:						
1925 to 1939	1934	15	27	30		
1898 to 1910	1904	13	47	46		
1851 to 1867	1858	17	45	44		
1806 to 1822	1814	17	45	53		
1761 to 1775	1761	15	30	21		
1731 to 1747	1740	17	_	_		

^a Peak years were maximum growth reduction years.

^b Intervals between outbreaks were computed as the number of years between initial years, and as the number of years between peak years of sucessive outbreaks.



Table 2—Species and numbers of trees sampled in each stand (continued)

Stand name	ID ^a	Species ^b	No. of trees	Inner date ^c	Outer date
Bally Mountain	BLMD	PSME	5	1703	1990
	BLMG	ABGR	13	1797	1990
	BLMP	PIPO	10	1469	1990
Eagle Cap, West:					
Minam River	MIRD	PSME	3	1712	1990
	MIRG	ABGR	18	1787	1990
	MIRP	PIPO	4	1675	1990
North Fork Minam River Eagle Cap, East:	NMRG	ABGR	24	1860	1990
Imnaha River N. Fork	NIMD	PSME	17	1672	1991
	NIMG	ABGR	11	1816	1991
	NIMP	PIPO	2	1796	1991
Indian Crossing	IDCD	PSME	7	1747	1990
	IDCG	ABGR	5	1842	1990
	IDCP	PIPO	14	1550	1990
Fish Lake	FLKD	PSME	5	1833	1990
	FLKG	ABGR	18	1835	1990
Fish Lake PIPO	FLPP	PIPO	22	1585	1991

^a Stand identifications correspond with those in figures 4 and 5.

^b Species Codes: ABGR = Abies grandis

PSME = Pseudotsuga menziesii
PIPO = Pinus ponderosa
LAOC = Larix occidentalis
PIEN = Picea engelmannii
PICO = Pinus contorta

tussock moth outbreaks, which usually continue for less than 5 years (Mason and Wickman 1989, Shepherd and others 1988, Wickman 1980, Wickman and others 1980), were preserved in the standardized ring-width index series.

5. Tree-ring chronologies from individual host trees (two core index series averaged) and the stand chronologies (averages of all cores from the same species within a stand) were compared with a nearby nonhost stand chronology. We visually examined overlay plots of host and nonhost tree-ring series on a computer screen and on paper. Comparisons also included computing Pearson correlation coefficients between the paired sets. These comparisons were used to determine if the host and nonhost were similar in their year-to-year variations, particularly between known outbreak periods in the 20th century, but different during known defoliator outbreaks.

TABR = *Taxus brevifolia*^c Inner and outer dates are earliest and latest measured tree rings, respectively, in each stand.

- 6. All host tree-ring chronologies were "corrected" by subtracting the nearby rescaled nonhost chronology. The nonhost chronology was rescaled by first multiplying each index value in the chronology by the ratio of the standard deviations of host and nonhost chronology indices for the common period (see Swetnam and others [1985] for equations).
- 7. The corrected host chronologies were then compared with forest insect survey records beginning in 1910 (Dolph 1980, Gast and others 1991, Mason, ¹ Shepherd and others 1988, Wickman and others 1973). Based on these observations, characteristics of the corrected series during known outbreaks of the two defoliators were used to establish a set of criteria (signatures) for identifying outbreaks in the tree-ring chronologies. The known budworm outbreaks within many of our sampled stands occurred from about the mid-1940s to late 1950s, and from 1980 to present. The known tussock moth outbreaks occurred during the mid-1940s and from 1972 to 1974.

In selecting these criteria, we also relied on published descriptions and comparisons of tree-ring index patterns caused by budworm and tussock moth defoliation (Brubaker 1978, Brubaker and Greene 1979, Wickman 1986, Wickman and others 1980). The basis of the criteria that, theoretically, would enable us to differentiate tussock moth defoliation effects from those of the budworm in tree-ring series from the same trees relates to outbreak patterns typical of these species. In particular, tussock moths tend to quickly defoliate large proportions of tree crowns within 1 to 2 years, and then the outbreak collapses within 3 to 5 years. Hence, the tree-ring series typically show sharply reduced growth persisting for about 3 to 6 years (a couple of years may be required for growth recovery after collapse of an outbreak). In contrast, tree defoliation by budworm typically builds up over several years, and outbreaks may last for a decade or longer. In these cases the tree-ring series often show growth reduction persisting for at least 8 years.

A computer program, OUTBREAK, was written by Holmes and Swetnam² to implement the correction procedure, to check each tree-ring chronology for the outbreak criteria, and to compile the results for each individual tree-ring series from each stand. The criteria used by the program for detecting the western spruce budworm signatures in the tree-ring series were as follows:

Growth was reduced below the mean of the series for at least 8 years. These 8
or more years of reduced growth may not be entirely consecutive; they may be
interrupted by a single year of increased growth above the mean of the series on
no more than one occasion before and no more than one occasion after the
maximum growth reduction year.

and

Mason, R.R. Unpubished data. On file with: Pacific Northwest Research Station, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850-3399.

² Holmes R.L.; Swetnam, T.W. Dendroecology program library: program outbreak user's manual. 5 p. Unpublished document. On file with: Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ 85721.

 Growth was reduced at least 1.28 standard deviations below the mean of the corrected tree-ring index series during at least one of the 8 or more years of the outbreak (values below 1.28 standard deviations comprise approximately the smallest decile of index values).

The criteria for estimating the duration of western spruce budworm outbreaks were:

- The beginning year of the outbreak was estimated to be the first year below the mean of the series during the identified outbreak period.
- The last year of an outbreak was estimated to be the last growth year below the mean of the series preceding the first of at least two consecutive years above the mean of the series. Alternatively, in the case where one year of growth above the mean of the series had already been included in the outbreak since the maximum growth reduction year (see criterion number 1) then the last growth year below the mean of the series preceding the next single year of growth above the mean of the series was estimated to be the end of the outbreak.

The criteria for detecting the Douglas-fir tussock moth signatures in the tree-ring series were:

Growth was reduced below the mean of the series for at least 4 consecutive years and not more than 6 consecutive years.

and

• Growth was reduced at least 1.28 standard deviations below the mean of the series during at least one of the years of the outbreak.

and

• The maximum year-to-year growth reduction (that is, the difference between consecutive index values during a detected outbreak) was at least 1.0 standard deviation units below the mean of the original corrected index series.

The criteria for estimating the duration of Douglas-fir tussock moth outbreaks were:

- The beginning year of the outbreak was estimated to be the first year below the mean of the series during the identified outbreak period.
- The last year of an outbreak was estimated to be the last reduced growth year preceding the first year above the mean of the series.

The above criteria were empirically based on accumulated observations and knowledge of the different characteristics of the life cycles of these insects and the tree-ring responses to them. For example, the threshold settings for magnitude of growth reductions identified by outbreaks were based on observations that the extreme low corrected indices were most consistently related to known outbreak events since the mid 1940s. This was because nonhost chronologies were not perfect climatic controls for growth in the host chronologies. Hence, the corrected series contained some "noise" due to differences between the host and nonhost tree-ring chronologies that were not related to defoliator outbreaks. The duration criteria were specific to typical patterns of budworm and tussock moth outbreak lengths and the amount of time that tree-ring growth was typically reduced as a result of defoliation (Brubaker 1978;

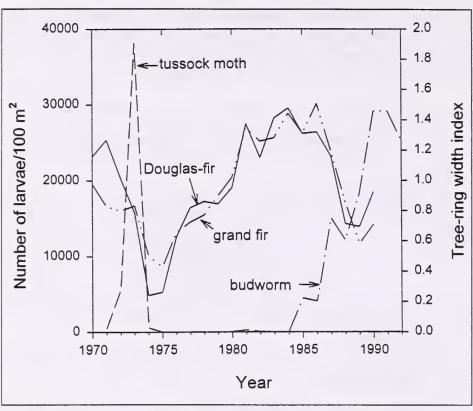


Figure 2—Comparison of larval density measurements (see footnote 1) and tree-ring index chronologies (1970 to 1992) from the Drumhill Ridge stand. A lagged tree-ring response to defoliation is evident.

Brubaker and Greene 1979; Swetnam and Lynch 1989, 1993; Wickman 1980, 1986). The criteria for identifying the duration and the beginning and ending dates for budworm outbreaks were designed to include some increased growth years, typically occurring near the beginning or ending of outbreaks, when budworm populations were slowly building or declining. Such temporary, relative increases in growth during an outbreak could be due to favorable climate overriding the negative effects of low levels of defoliation, or because the insect populations briefly declined then increased. The criteria for a maximum growth rate reduction threshold in the case of tussock moth (criterion number 3) was based on our own observations (for example, fig. 2) and Brubaker's findings that this species tends to initially cause a greater year-to-year decrease in ring growth than budworm (Brubaker 1978, Brubaker and Greene 1979).

Although the criteria were designed to identify tussock moth and budworm-type treering signatures, they do not produce an exclusive identification of either a tussock moth or a budworm outbreak for a particular period. In other words, different outbreaks may be identified as having only a budworm-type signature or only a tussock moth-type signature, or both. As discussed below, with the current criteria we cannot clearly distinguish tussock moth effects from budworm effects during some outbreaks.

Comparison of the host and nonhost tree-ring chronologies generally confirmed that the three species had similar year-to-year growth variations, but that growth trends diverged sharply during periods of known budworm or tussock moth outbreaks in the late 20th century (fig. 3). Many reduced growth periods in earlier times were probably also due to outbreaks (fig. 3). Growth increases (or releases) between outbreaks also were observed, as in other studies (Swetnam and Lynch 1989, 1993; Wickman 1980). These increases in growth were partly an artifact of the standardizing procedure, which established a mean level approximately midway between maximum and minimum growth levels. Visual inspection of the increment cores and measured time

Results

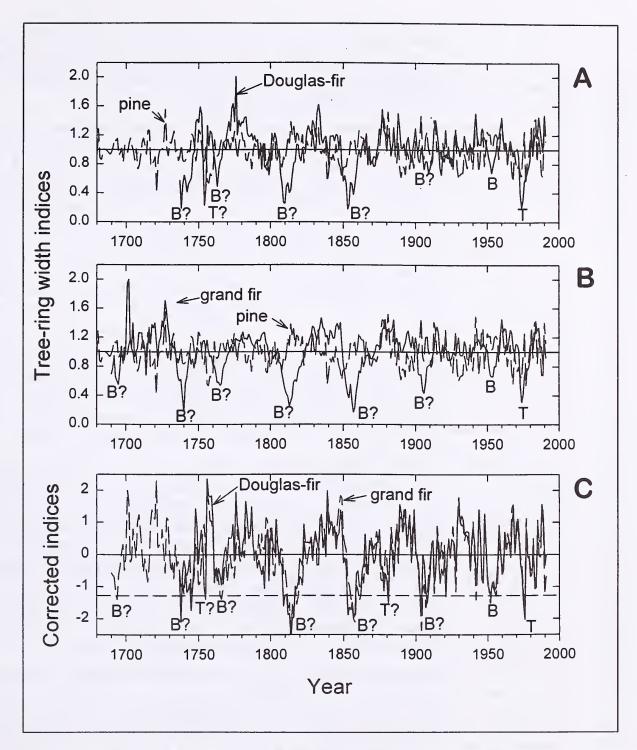


Figure 3—Overlay plots of the Grizzly Bear Meadow Douglas-fir and grand fir tree-ring index chronologies and the Cross Canyon ponderosa pine chronology (parts A and B). Sharply reduced growth periods in the Douglas-fir and grand fir are visible corresponding to known and inferred outbreaks of western spruce budworm (B) and Douglas-fir tussock moth (T). Inferred outbreaks are shown with a question mark. Part C shows the corrected tree-ring indices (standard deviation units) for the Douglas-fir and grand fir, produced by subtracting a rescaled version of the pine chronology. The dashed horizontal line is the 1.28 standard deviation threshold. Not all possible outbreaks, based on the threshold, are obvious in the overlay comparisons (A and B), but they appear more clearly in the corrected version (C).

series showed, however, that many of these increases were actually large-magnitude growth releases. These releases probably were due to a combination of reduced competition from trees killed during the previous outbreaks and nutrient recycling in the soils from foliage, insect bodies, and frass.

The most recent tussock moth outbreak occurred from 1972 to 1974 in many of our sampled stands. This was observed as a sharply reduced growth period lasting less than 6 years. When compared with larval density data from some of the stands (see footnote 1), a lag of 1 to 2 years was observed in the ring-growth depressions after the peak in larval densities (fig. 2). Such a lag in radial growth response to defoliation, especially in the lower bole, also has been noted in previous tree-ring studies (Alfaro and others 1985, Brubaker and Greene 1979, Wickman and others 1980). Unabated cambial growth in the lower tree bole (where increment cores were taken) during the first year of defoliation may be due to the presence of adequate stored food reserves in local xylem and phloem tissues from growth in the previous year (Fritts 1976).

The most recent budworm outbreak occurred in all stands during the early 1980s. This outbreak and an earlier one during the mid-1940s to late 1950s were easily identified in stands where they occurred (figs. 3, 4, and 5), although lags of 1 to 3 years were observed in the response of single trees to this event. Furthermore, the occurrence of these reduced growth periods generally matched both the spatial and temporal record of occurrence of defoliation (Dolph 1980).

As observed in previous tree-ring studies, the corrected series tended to show the timing of known and inferred outbreaks more clearly than either examinations of the host series alone or comparisons of overlay plots of the host and nonhost series (figs. 3, 4, and 5). We also found that careful examination of both the corrected tree chronologies and the corrected average stand chronology for each stand was the most effective way to confidently identify past defoliation episodes (fig. 6). (The corrected tree chronologies were derived by averaging the two core index series from each tree and then correcting each with the local pine stand chronology; the corrected stand chronologies were derived by averaging all core index series from a species within each stand, and then correcting these series with the local pine chronology.)

Examination of individual corrected tree chronologies was helpful, because the effects and timing of some outbreaks were very pronounced on some trees as extremely reduced growth persisting for a period of years, but other trees (usually a minority) were only slightly affected or not at all affected during the same period. This pattern is actually observable in the field today; even the most heavily defoliated stands usually contain some trees with little or no damage. Thus, the corrected stand chronologies sometimes averaged out the defoliation signal when some of the trees in the stand were not significantly affected by the defoliation event.

Episodic outbreaks were visually obvious in the regional summary of all sampled and analyzed host trees and stands (fig. 7). The tree compilation (upper plot in fig. 7) seemed to have somewhat better temporal resolution; the outbreak beginning, peak, and ending years were more sharply defined than in the stand compilation (lower plot in fig. 7). Although several chronologies extend back to the 1700s and earlier, the first decades of these chronologies usually contained fewer than five trees. Our confidence in patterns during this period was relatively low. Most of the longer chronologies had adequate sample depth (that is, more than about five trees) for making confident interpretations after about 1800. Most of the shorter chronologies had adequate sample depth after about 1850.

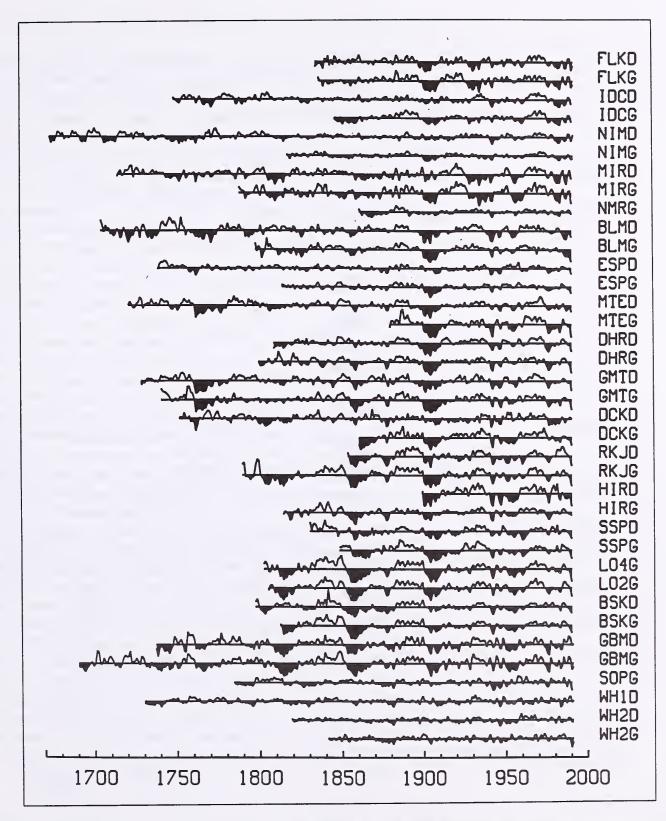


Figure 4—Corrected tree-ring index chronologies (average of all trees sampled within stands) from the Blue Mountains and the Eagle Cap Wilderness, northeastern Oregon, 1670-1991. Paired chronologies of Douglas-fir and grand fir for most stands are shown (see site identifications in table 2; the last letter in the site identification on the right side of the figure indicates Douglas-fir [D] and grand fir [G]). All growth reduction values below the mean lines (index value of 1.0) are shaded, but identified outbreaks are typically the larger and sustained growth reduction years. The index values (y-axis) range from about 0.0 to 2.5.

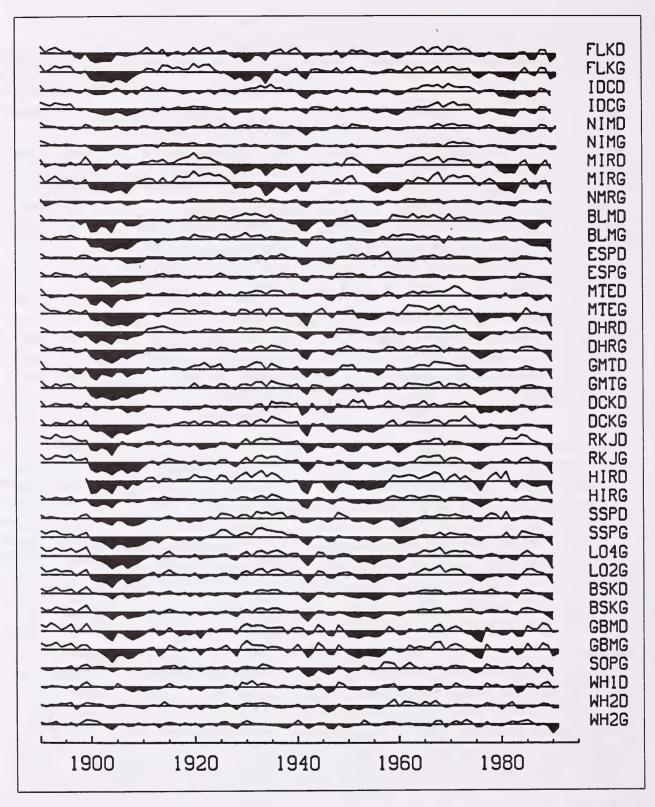


Figure 5—Corrected tree-ring index chronologies (average of all trees sampled within stands) from the Blue Mountains and the Eagle Cap Wilderness, northeastern Oregon, 1890-91. These are the same series shown in figure 4 but are for the last century only.

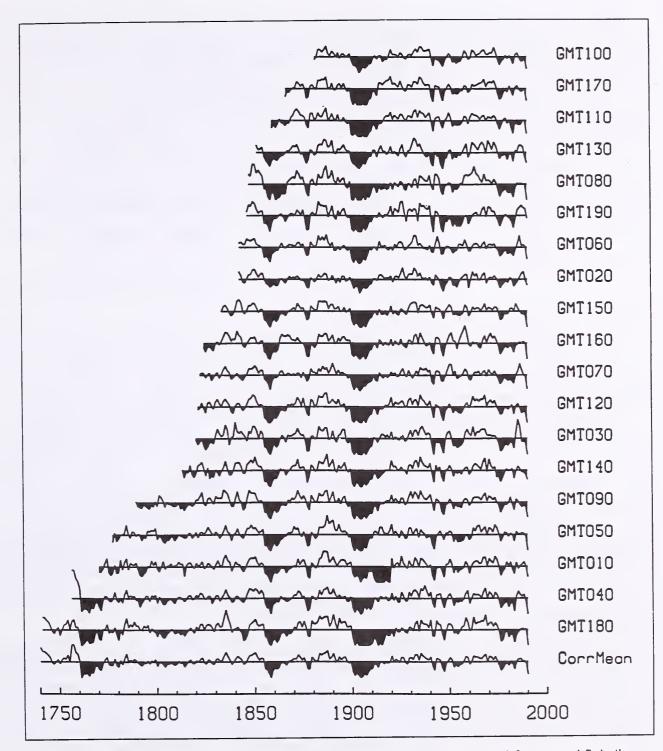


Figure 6—Corrected tree-ring index chronologies (averages of two cores per tree) from grand fir in the Green Mountain stand. The lowermost plot is the stand chronology; that is, the average of all the tree chronologies.

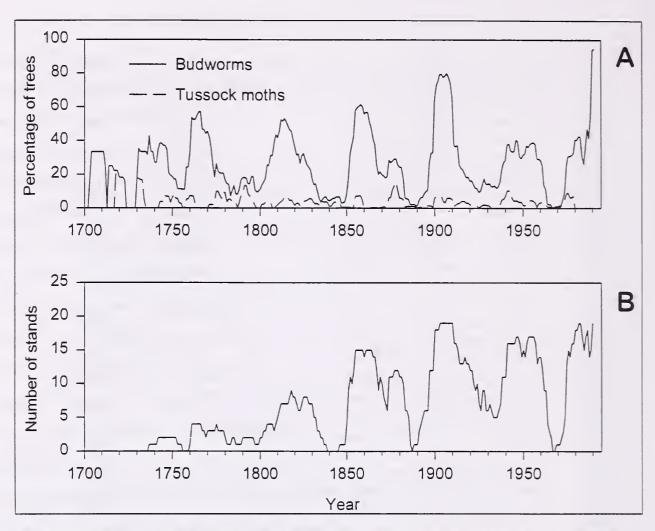


Figure 7—Summary of the percentage of individual trees (A) recording either western spruce budworm or Douglas-fir tussock moth tree-ring signatures relative to all sampled trees for Douglas-fir and grand fir combined (1700-1991). Part B shows the number of stands recording budworm-type tree-ring signatures among a total of 21 sampled stands. In this summary, a stand was counted as recording an outbreak if two or more sampled host trees in that stand (either Douglas-fir or grand fir) showed a budworm-type signature.

Budworm and tussock moth effects often were not consistently distinguishable. For example, the budworm curve shows increased activity throughout the 1940s, but the available documentary records suggest that defoliated areas greatly increased only after about 1946 or 1947 and peaked around 1950. The documentary record before 1946 or 1947 was incomplete. Although forest entomologists were observing and reporting on insect activity in this region since the 1930s, it is probable that during World War II (1941-45) personnel shortages prevented thorough surveys. The records did report active tussock moth activity for a short period in some isolated areas after 1946, particularly in an area west of Troy, Oregon, near and around several of our stands (Wenaha 1 and 2, Soap Springs, and possibly Grizzly Bear Meadow) (Dolph 1980, Gast and others 1991, Shepherd and others 1988, Wickman and others 1973).

Relatively large, short-term differences between the host and nonhost tree-ring chronologies occasionally were observed. The periods from about 1878 to 1880 and 1941 to 1942, for example, had sharply reduced corrected index values (figs. 4 and 5). The period 1878 to 1880 precedes the documentary record, and we have not found any documentary evidence to confirm that a widespread outbreak, either of budworms or tussock moths, occurred during the early 1940s in this area. In both cases, the growth

index values of the host trees (uncorrected) were not reduced below the long-term mean (an index value of about 1.0 in these standardized series), but they often were much lower than growth indices of the nonhost trees. In other words, it appears that the nonhost trees responded vigorously to favorable conditions during these years, whereas the host radial growth increased only moderately or stayed about the same as the long-term mean. We cannot conclusively identify the causes of these relatively large, short-term, species-related differences. It is interesting to note, however, that the years 1940 and 1941 were extremely wet, especially in the fall and winter (meteorological records do not extend back to the 1870s). Perhaps extremely wet conditions during certain seasons tend to provide relatively more favorable growing conditions for ponderosa pine than for Douglas-fir in this region. Fritts (1976), for example, demonstrated that ponderosa pine in the Western United States typically has a stronger positive response than Douglas-fir to fall and winter precipitation preceding the cambial growth season.

The 1972 to 1974 tussock moth outbreak was misidentified, as a budworm outbreak in many trees, which caused the budworm curve to rise too soon in figure 7. Many of the tussock moth impacts persisted throughout the 1970s, and then beginning in the early 1980s, defoliation by budworm caused ring growth to remain low. Thus, the resulting long periods of reduced growth were erroneously identified by the OUTBREAK program as budworm outbreaks. We also noted that maximum growth reductions during the 1972-74 tussock moth event were often not as large as during the late 1940s event.

The 1980s budworm outbreak appeared as reduced growth in the early to mid 1980s, a brief recovery was documented in many stands, and then growth declined again in the late 1980s or early 1990s. The last few years of the chronologies (1988-91) had the highest proportion of trees recording an outbreak (fig. 7). Like the 1950s outbreak, the peak number of trees recording the 1980s outbreak lagged by several years the peak in defoliation estimated from the documents.

When assessing and interpreting these patterns, it is necessary to consider that the characteristics and effects of modern defoliation events (post-1947) on the tree-ring series could have been significantly affected by insecticide use in this region. More than 1.7 million ha. were sprayed with DDT in Oregon from 1948 to 1958 for control of budworms, and about 162 000 ha were sprayed in 1974 to control tussock moth (Graham and others 1975). About 17 000 ha were sprayed with other pesticides from 1976 to 1979 (Dolph 1980). Because many of our stands were treated, the reduced magnitude of the outbreaks of the late 1940s to 1950s and the 1970s (as measured by proportion of trees recording an outbreak, figs. 4 to 7) could be due to intensive and extensive pesticide use.

Discussion

The effects of defoliation by budworms or tussock moths were easily seen on some increment core samples and in measured tree-ring width series as sharply reduced growth periods often followed by growth releases. Budworm and tussock moth effects were more subtle and difficult to identify in other samples from host trees, requiring a direct comparison with nonhost tree-ring series to confidently determine the timing of past outbreaks. The correction procedure using the nonhost pine chronologies gave us an objective basis for determining that reduced growth periods were due to defoliation by insects and not directly to climate. Budworm and tussock moth were expected to have different tree-ring signatures because they usually defoliate trees at different

rates and persist for different lengths of time within forest stands. We encountered problems in consistently differentiating recent and past outbreaks of these defoliators, however, particularly when outbreaks were contemporaneous or closely spaced in time.

The corrected radial growth series showed a lag response of one to several years in relation to known initiation, maximum, and decline years in insect population numbers and areas defoliated. These lag responses increased the difficulty of separating the effects of different outbreaks. Furthermore, in two instances (ca. 1878-80 and 1941-43) during the past 300 years, we observed short-term differences between host and nonhost trees that we suspect may represent short-term differences in climatic responses, rather than tussock moth or budworm effects. Given these uncertainties, we summarize our interpretations of the timing and duration of defoliation events back to about 1730 (table 3), as derived from examination of individual tree and mean stand chronologies (figs. 4 to 7).

We have less confidence in our estimates of past tussock moth outbreaks, than budworm outbreaks because we were not always able to distinguish the relatively shortterm effects of tussock moths from short-term climatic differences between the host and nonhost trees. Two tussock moth outbreaks in this region were documented by forest surveys (ca. 1945-47 and 1972-74). The effects of both outbreaks were observed in the tree-ring series (figs. 3 and 5), but they were partly confounded in the output of the OUTBREAK program by overlap between the possibly spurious "outbreak" from about 1941 to 1943 and the known mid-1940s tussock moth outbreak, and by the overlap of the effects of the 1970s tussock moth outbreak and the 1980s budworm outbreak (fig. 7). We are more confident that the longer lasting outbreaks (those greater than about 10 years duration) observed in the mean site-corrected indices (figs. 4, 5, and 6), and as compiled from individual tree series by the program OUTBREAK (fig. 7), were at least partly caused by budworm outbreaks. In all cases, these periods were relatively long lasting and often severely suppressed growth in the host trees that was not matched in the nonhost trees. Because we had greater confidence in the budworm than the tussock moth outbreak estimates, we compiled duration and intervals between regional budworm outbreaks only (table 4).

The mixed results from the OUTBREAK program indicated that additional refinement of the criteria for distinguishing tussock moth from budworms is required. This program is essentially an empirical model of radial growth response to tussock moth and budworm defoliation. Additional tuning (or calibration) of the criteria based on the study of insect population data and tree-ring responses within stands might result in improved performance of the model. Sorting and comparison of the tree-ring responses by the two host species—Douglas-fir and grand fir—might also offer some new insights because of the differences in host preference by the two defoliators (Carolin and Coulter 1972, Wickman 1978, Williams 1967). Other basic differences between budworm and tussock moth outbreaks may require different sampling strategies. In the 20th century, tussock moth outbreaks typically have occurred in smaller patches distributed over the landscape than have budworm outbreaks (Mason and Wickman 1989, Shepherd and others 1988). Thus, detection of regional patterns of tussock moth occurrence may require more extensive tree-ring sampling.

Table 3—Interpretations of timing and duration of western spruce budworm and Douglas-fir tussock moth outbreaks in the Blue Mountains and Eagle Cap Wilderness as estimated from tree-ring chronologies, 1730 to 1991

Outbreak period and peak year^a

Notes

Modern, known outbreaks:

1980 to present

(1986)

The current budworm outbreak was continuing or resurging at time of sampling in most stands (1990-91). It appears as reduced growth in the early 1980s in most stands, particularly the Eagle Cap stands. A brief recovery occurred in many stands in 1984 or 1985, then growth was reduced again. Low growth from the 1972-74 tussock moth outbreak continued until about 1980 in some stands, overlapping the effects of the 1980s budworm outbreak and so appearing as one long outbreak from the 1970s to mid 1980s.

1972 to 1974

(1973)

A tussock moth outbreak appears in tree rings as reduced growth from about 1973 to 1977 and as late as 1980 in

most stands.

1946 to 1958

(1950)

A budworm outbreak appears in tree rings as reduced growth period from about 1946 or 1947 to about 1960. The early period after about 1946 may be confused in some stands with a tussock moth outbreak that occurred

from about 1945 to 1947.

1945 to 1947

(1946)

A tussock moth outbreak appears as a short, reduced growth period from about 1946 to 1948 or 1949, but this outbreak is confirmed only by forest survey records in a few stands in the Blue Mountains, Wenaha group (table 1, fig. 1), hence it might be confused with rising budworm defoliation occurring at about the same time. Absent in Eagle Cap stands.

Inferred outbreaks:

1925 to 1939

(1934)

A budworm outbreak was identified only in Eagle Cap stands; among these stands it was somewhat longer lasting at Minam River, less pronounced at Indian Creek, and not present in the Imnaha stand.

Table 3—Interpretations of timing and duration of western spruce budworm and Douglas-fir tussock moth outbreaks in the Blue Mountains and Eagle Cap Wilderness as estimated from tree-ring chronologies, 1730 to 1991 (continued)

Outbreak period and peak year ^a	Notes
1927 to 1929 (1928)	A tussock moth outbreak with a relatively weak signature showing clearly only in the Blue Mountains, Wenaha group.
1898 to 1910 (1904)	A budworm outbreak with a very strong and clear signature in most trees and stands; beginning in many stands in 1900. Some stands show a possible tussock moth outbreak or a resurgent budworm outbreak in 1913 to 1914 following brief recovery years of 1911 and 1912.
1851 to 1867 (1858)	A budworm outbreak appears with a strong signature in some northern and central Blue Mountains stands, but appears weaker, shorter, or not clearly present in other stands in the region. Short growth reduction periods in some trees and stands have tussock moth signatures.
1806 to 1822 (1814)	A budworm outbreak in some of the northern and central Blue Mountains stands and in the Imnaha and Minam River stands in the Eagle Cap Wilderness. A somewhat earlier event in 1800s also appears in Dry Creek and Big Sink stands.
1761 to 1775 (1761)	A budworm outbreak appears to have occurred widely in the Blue Mountains, but only a few trees are included in the chronologies in any of the stands extending back this far in time, so timing, extent and duration of this outbreak are very tentative.
1731 to 1747 (1740)	A budworm outbreak is evident in only a few trees in Grizzly Bear Meadow that extend back in time far enough to clearly show this outbreak

^a Peak year shown in parantheses

Table 4—Estimate of timing, duration, and intervals between western spruce budworm outbreaks from tree-ring chronologies

		Peak year ^a Outbreak duration		Intervals between outbreaks ^b		
Outbreak period	Peak year ^a			Peak		
		No. of y	ears – – – –			
Modern, known outbreaks:						
1980 to present	1986	14	34	36		
1946 to 1958	1950	13	21	26		
Inferred outbreaks:						
1925 to 1939	1934	15	27	30		
1898 to 1910	1904	13	47	46		
1851 to 1867	1858	17	45	44		
1806 to 1822	1814	17	45	53		
1761 to 1775	1761	15	30	21		
1731 to 1747	1740	17	_	_		

^a Peak years were maximum growth reduction years.

Comparison of the duration of growth reduction periods caused by budworm outbreaks indicated relatively little variability (range: 13 to 17 years, table 4). Lags in radial growth response to tree defoliation at the beginning of outbreaks might be somewhat offset by lags in recovery of tree-growth to the long-term mean level (or above) at the end of outbreaks. Duration of the reduced growth therefore may be a reasonable approximation of outbreak duration. Further observations and comparisons of insect populations and tree-ring responses on individual trees and within stands are needed to test this idea.

The compilation of intervals between outbreaks over the past several hundred years (table 4) suggests that some temporal changes in the length of intervals between outbreaks (or frequency) may have occurred. Between about 1775 and 1898, the intervals between inferred outbreaks ranged from about 45 to 53 years. After 1910, the intervals between the outbreaks ranged from about 21 to 36 years (including the 1920s to 1930s outbreak in the Eagle Cap Wilderness Area). A relatively short interval of about 21 to 30 years occurred between the inferred outbreak of the 1730s to 1740s and the subsequent outbreak of the 1760s to 1770s, but the earlier outbreak is identified in only three stands; hence, it is not clear whether the 1730s to 1740s outbreak

^b Intervals between outbreaks were computed as the number of years between initial years, and as the number of years between peak years of sucessive outbreaks.

should be considered "regional" or "subregional." The earliest possible outbreaks (pre 1740s) visible in the chronologies (figs. 4 and 7) must be considered to be only tentative evidence because of the sparseness of the tree-ring record in these earliest periods. Generally, the earliest periods of the oldest chronologies are represented by only one or a few trees.

The 1920s to 1930s outbreak was recorded only in the Eagle Cap Wilderness stands and thus is reflected only as a small peak in the regional summaries (fig. 7). The discovery of this outbreak is important because, if it is included in the regional summaries it raises the total number of 20th century outbreaks within the entire region to four (counting the 1900s outbreak which began in about 1898). If the 1920s to 1930s outbreak is not included, then the intervals between outbreaks in the 20th century appear to be more similar to those in earlier centuries. Recent analyses of 14 additional stands in the southern Blue Mountains) indicated that the 1920s to 1930s outbreak was widespread and relatively intense in this portion of the region.³

The most recent outbreak (1980s to 1990s) is recorded as a severe growth reduction in the largest proportion of trees sampled (figs. 4, 5, and 7). This finding also supports the hypothesis that a change has occurred in outbreak dynamics. The recent outbreak may not have run its complete course within the stands at the time of sampling (1990 or 1991), so even greater reductions (or recovery) may have occurred since that time. The early 1900s outbreak and the 1850s to 1860s outbreaks also appeared to have been long lasting and relatively severe in terms of growth reduction in survivor trees. The late 1940s to 1950s budworm outbreak appears to have been one of the mildest outbreaks in the past two centuries. As previously pointed out, however, the intensive insecticide spraying during this outbreak probably reduced the severity of its effects on survivor trees.

Outbreaks were typically synchronous across the entire northern Blue Mountain region (with some important exceptions, such as the 1920s to 1930s outbreak) during the period of record represented by most of the sampled trees and stands (about post-1800). These findings contrast with our tree-ring/western spruce budworm studies in the southern Rockies, where outbreaks generally appear to be more wide-spread and severe in the late 20th century than during earlier centuries (Swetnam and Lynch 1989, 1993). We did not detect any obvious changes in the frequency of outbreaks in the 20th century in the southern Rockies.

Our tree-ring reconstructions document only one measure of outbreak severity within forest ecosystems: the radial growth of surviving trees. We do not know, for example, how much understory or overstory tree mortality was caused by past outbreaks. Tree mortality caused by subsequent attack of weakened trees by bark beetles is also an important factor in the dynamics of these stands (Wickman 1992). Losses due to topkilling and cone crop reduction are unknown. Despite these unknowns, given that the recent budworm outbreak in some Blue Mountain stands resulted in mortality rates exceeding 80 percent of all overstory trees, it seems highly unlikely that such stands could have sustained similar mortality rates during the many previous outbreaks that occurred in this region.

³ Swetnam, T.W.; Wickman, B.E. Unpublished data. On file with: Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ 85721.

Conclusions

Our success at separating the effects of climate, budworm, and tussock moth defoliation on tree-ring growth was mixed. Lagging effects of tree-ring response to defoliation and dissimilar climatic responses of the host and nonhost species are important limitations and causes of the inaccuracies of the methods we applied. Different spatial and temporal patterns of tussock moth versus budworm outbreaks, such as extensiveness and duration of impacts, may require different or expanded tree-ring sampling strategies. For example, data from more stands and host trees are needed to clearly identify historical, regional tussock moth patterns because outbreaks may have occurred within smaller areas than budworm outbreaks. We are currently analyzing new collections from the southern Blue Mountains and the Mount Hood and Willamette National Forsts that we plan to describe in future publications. We expect that refinement of our understanding from observations and modeling of the climate and defoliation responses of host and nonhosts species will result in improvements in the tree-ring estimates of past insect population dynamics.

Our tree-ring-reconstructed history provides strong evidence that outbreaks have recurred repeatedly in the northern Blue Mountains for at least three centuries. The frequency of outbreaks throughout the entire region may have increased in the 20th century relative to earlier centuries. Three or four budworm outbreaks were identified in the 20th century versus two or three in the 19th and 18th centuries. A relatively high proportion of trees had reduced radial growth (fig. 7), and there were high levels of tree mortality in many Blue Mountains stands during the 1980s to present outbreak (Mutch and others 1993, Wickman 1992). Altogether, these findings generally lend support to the hypothesis that a change in budworm outbreak dynamics occurred during the 20th century. Although this is a reasonable conclusion based on currently available data, the number of regional events included in our reconstruction was too low to carry out statistical hypotheses tests. Furthermore, inclusion or exclusion of possibly subregional events (such as the 1920s to 1930s outbreak) changes the assessment of outbreak frequency. These patterns reflect the importance of scale considerations in landscape ecology (Allen and Hoekstra 1993). In this case, at the larger spatial scale of the entire Blue Mountains region, outbreak frequencies appear to have increased in the 20th century relative to earlier centuries, but at the smaller spatial scales of the northern Blue Mountains (excluding the Eagle Cap Wilderness), the evidence for such change may be equivocal.

Extrapolation of our findings from a network of selected stands within the Blue Mountains to the overall landscape may ultimately require a modeling approach using geographic information systems. We plan to expand our sampling in the future, and to study intervals between outbreaks within all the individual stands that we have studied. This may provide a large enough pooled sample size for statistical tests of temporal and spatial differences in outbreak regimes.

The possible direct and indirect causes of any changes in outbreak dynamics are not specifically tested with these data. Grouping of subregional sets of data or sorting by differences in land-use history may provide some insights into the possible influence of past harvesting practices or fire history (Wickman and others 1994). Comparison of outbreak occurrence data with climatic data also may reveal important associations (see, for example, Swetnam and Lynch 1993).

Assessments of tree mortality patterns and studies of stand age structure and composition at landscape scales also are needed to address questions regarding overall impacts and dynamics of past and current outbreaks. Although such data are not currently available, it seems highly unlikely that 19th century or earlier outbreaks decimated the old-growth stands that we sampled, at least not to the extent that they have been in the most recent outbreaks. It is more likely that episodic outbreaks played an important role in sustaining the long-term vigor and stability of these stands by enhancing nutrient cycling and regulating primary productivity (Haack and Byler 1993, Mattson and Addy 1975, Schowalter and others 1986). Defoliator-caused mortality of shade-tolerant host trees in the understory (Wickman 1978) may have served a similar and complementary role to that of surface fires (Holling 1981). The resulting low fuel accumulations and continuity in mixed-conifer stands repeatedly "thinned" by low intensity insect outbreaks and surface fires probably prevented or postponed catastrophic stand replacement by high-intensity outbreaks or fires.

Metric Conversions

- 1 hectare (ha) = 2.47 acres
- 1 meter (m) = 3.28 feet
- 1 kilometer (km) = 0.62 mile
- 1 square meter per hectare $(m^2/ha) = 4.36$ square feet per acre

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Dendroecology methods were used to reconstruct a three-century history of western spruce budworm and Douglas-fir tussock moth outbreaks in the Blue Mountains of northeastern Oregon. Comparisons of 20th century Forest Service documentary records and host and nonhost tree-ring width chronologies provided an objective basis for distinguishing climatic effects from insect-caused defoliation effects. Budworm outbreaks were more confidently reconstructed than were tussock moth outbreaks. Since A.D. 1700, at least eight regional budworm outbreaks have occurred at intervals of about 21 to 53 years. Reduced radial growth caused by defoliation lasted from about 13 to 17 years. Two regional budworm outbreaks occurred during the 19th century, and at least three and possibly four regional outbreaks have occurred during the 20th century. These findings generally support the hypothesis that budworm outbreaks have increased in frequency and severity in the 20th century in northeastern Oregon.

Keywords: Western spruce budworm, Douglas-fir tussock moth, tree rings, Blue Mountains, forest health, dendroecology.

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